

Mustelid and viverrid remains from the Pleistocene site of Cooper's D, Gauteng, South Africa

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Received 20 July 2013. Accepted 8 November 2013

Fossil mustelids and viverrids are rare in the African Pleistocene fossil record. The careful examination of sieved sediments from the well-dated Cooper's D locality in Gauteng has revealed six new mustelid and viverrid specimens. These represent three uncommon genera – two mustelids, *Propoecilogale bolti* and *Mellivora capensis*, and a viverrid, *Civettictis* cf. *civetta*. We describe and figure these six specimens here. Cooper's D is only the fourth African locality at which *P. bolti* has been identified, and it is the first of the Witwatersrand sites to contain remains of the African civet.

Keywords: *Civettictis*, *Mellivora*, *Propoecilogale*, civet, honey badger, weasel.

INTRODUCTION

Remains of members of the Mustelidae (weasels and badgers) and Viverridae (civets and genets) are not common in African Pleistocene deposits (Werdelin & Peigné 2010). Here we report on new material from both these families from Cooper's D, Gauteng. Cooper's D is dated to 1.4–1.5 Ma by U-Pb (De Ruiter *et al.* 2009). Known for the presence of *Paranthropus robustus* and unusually large accumulations of carnivores, suids and *Theropithecus oswaldi* for a southern African site, the published faunal list is extensive (De Ruiter *et al.* 2009). The presence of decalcified breccia in combination with a comprehensive sieving regime has resulted in the recovery of large numbers of smaller mammal bones, and as more of this material has been examined a number of additional taxa have been identified. Amongst these are the six specimens being described here.

METHODS

All specimens were identified using the modern and fossil comparative collections in the Bernard Price Collections housed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, and Ditsong National Museum of Natural History, Pretoria. The Cooper's D material is held within the Bernard Price Collection (BPI), with the site prefix CD. The Kromdraai B (KB) collection and the Archaeozoology (AZ) collection are both housed at the Ditsong Museum, Pretoria. Comparisons with fossil taxa that were not available in these collections were undertaken by comparison with the literature (e.g. *Mellivora benfieldi* in Hendey (1978)).

DESCRIPTION OF THE COOPER'S D MUSTELIDAE

Systematic palaeontology

Order Carnivora Bowdich, 1821

Family Mustelidae G. Fischer, 1817

Genus *Propoecilogale* Petter, 1987

Propoecilogale bolti (Cooke, 1985)¹

Material

CD 3896, right mandibular fragment with M₁ and alveoli for the P₄ and M₂ (Fig. 1a,b,c).

Description

A complete M₁ is present in a gracile mandible fragment. The M₁ has an oval basal contour and is transversely compressed and extremely narrow. The protoconid is centrally located on the buccal side and joined lingually to the base is a minute metaconid. The paraconid is short, only slightly higher than the talonid, but the same length as the protoconid and carinate. The talonid is short and quadrangular with an elongated and carinate hypoconid. The talonid is depressed into a valley that opens at the base of the metaconid.

Discussion

The very small M₁ and gracile mandible of CD 3896 is indistinguishable from the descriptions and photographs of *P. bolti* given by Petter (1987) and Werdelin & Dehghani (2011). The only difference is that the illustrations given by Petter (1987, p. 208) for *P. bolti* would suggest that the metaconid is more developed in this species than observed in the Cooper's material. The mesiodistal length of the M₁ is larger than observed in *P. bolti* and closer to the M₁ in *Poecilogale albinucha* (Table 1). This specimen is beyond question not *P. albinucha* as the metaconid is absent in this species. It is possible, given the larger size of the Cooper's material and the possibly more reduced metaconid, that this fossil represents a further step

¹The taxonomy of this extinct fossil weasel is somewhat confused. Petter, in Petter & Howell (1985), mentions that she will be naming a new genus of weasel based on the Laetoli material, and will include the specimens described by Cooke (1985) within it, as *Prepoecilogale bolti* (Petter & Howell 1985, p. 142). However, there is no description of the genus in that paper. The full generic description was published in Petter (1987), in which the spelling had been changed to *Propoecilogale bolti*. Since then, authors have used both spellings and also both references as the authorities for the taxon. Our reading of the ICZN code suggests that without the description, *Prepoecilogale bolti* is a *nomen nudum*, and was therefore superseded by *Propoecilogale bolti*. Hence we have referred the Cooper's D material to *Propoecilogale*.

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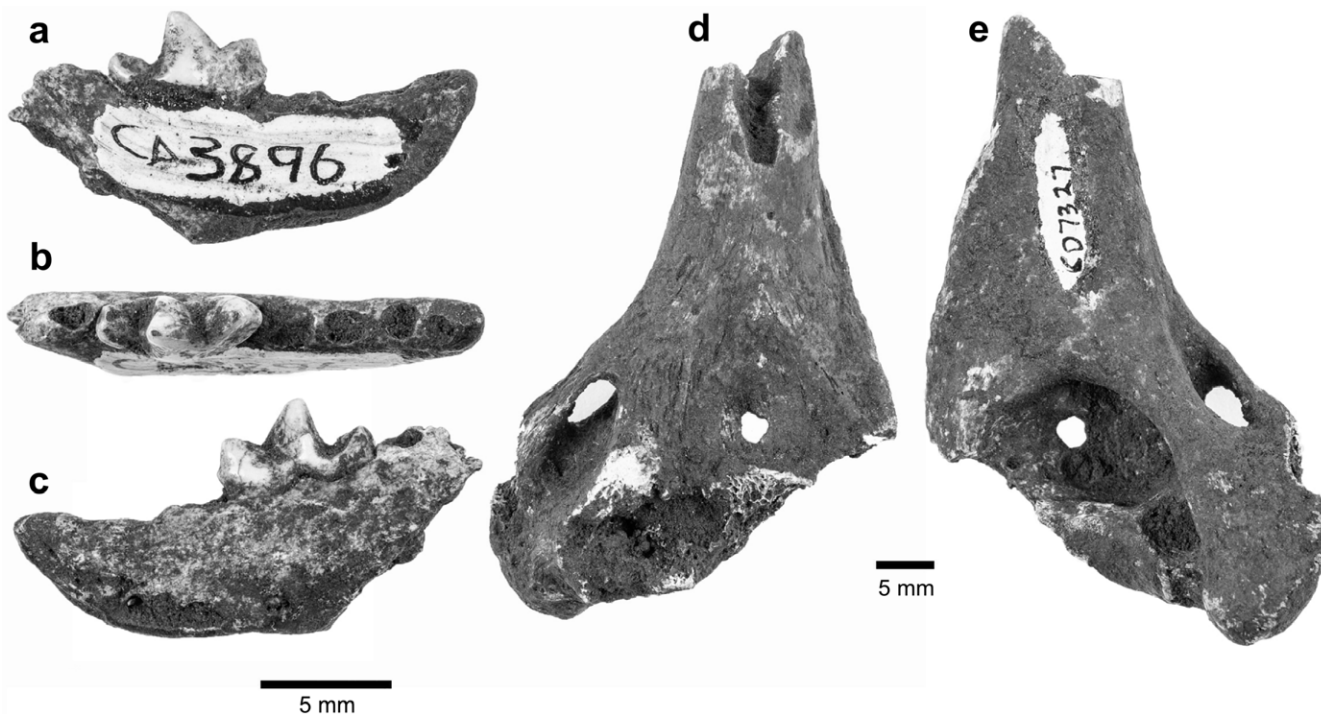


Figure 1. Mustelid material from Cooper's D. Specimen CD 3896, a right mandible fragment of *Propoecilogale bolti*, is shown in buccal (a), occlusal (b), and lingual (c) views. Specimen CD 7327, a distal left humerus of *Mellivora capensis*, is shown in ventral (d) and dorsal (e) views.

towards the modern species than the Laetoli material. This being the case it may be more appropriate to name a new species of small mustelid. However, based on the scarcity of material and the placement of it within the *Propoecilogale* – *Poecilogale* lineage we feel that the Cooper's material is best assigned to *P. bolti* for the time being. Note that the type specimen of *P. bolti* is a cranium (Cooke 1985) and therefore cannot be directly compared to the Cooper's D specimen. However the identification and extensive description of *Propoecilogale bolti* at Laetoli (Petter 1987) was based on both maxillary and mandibular dentition. The inclusion of *Poecilogale albinucha* in the faunal list given in De Ruiter *et al.* (2009) was based on the specimen described here. With the assignment of CD 3896 to *Propoecilogale*, there is now no record of *Poecilogale* at Cooper's D.

Genus *Mellivora* Storr, 1780

Mellivora capensis (Schreber, 1776) – Honey badger

Material

CD 7327, a left distal humerus fragment (Fig. 1d,e).

Description

A single specimen of *Mellivora* is identified in the Cooper's D collection. CD 7327 is a partial distal humerus comprising one quarter of the shaft, the olecranon fossa and the medial epicondyle – both condyles are missing (possibly gnawed off). No standard measurements can be taken of this specimen. A strong flange is present above the lateral epicondyle, and extends along what remains of the shaft. The supracondylar foramen is more visible on the dorsal surface than in the two modern specimens available for comparison. The olecranon fossa is quite low, and the specimen is very broad and flattened dorsally.

The articulation is deeply recessed within the olecranon fossa, whereas in the otter, *Aonyx capensis*, the only other extant mustelid of comparable size, it is much more dorsally placed. The presence of a foramen within the olecranon fossa is a variable feature in modern specimens; there is a hole in the fossa of CD 7327 but this appears to be damage rather than a natural perforation. It is a good match for modern *Mellivora capensis*, and is closer in size to a modern male than a modern female.

Discussion

Members of the genus *Mellivora* are rare at the Witwatersrand sites, with craniodental remains from Swartkrans Member 2 having previously been described as *Mellivora cf. sivalensis* (Hendey 1974a), and a distal humerus (KB 3258) from Kromdraai B identified as *Mellivora* sp. (Gommery *et al.* 2008). The Cooper's specimen (CD 7327) is very similar to both the modern honey badger and the Kromdraai B specimen and is here referred to *Mellivora capensis*.

DESCRIPTION OF THE COOPER'S D VIVERRIDAE

Family VIVERRIDAE Gray, 1821

Genus *Civettictis* Pocock, 1915

Civettictis cf. civetta (Schreber, 1776) – African civet

Material

CD 15667, left P⁴ (Fig. 2c,d,e; Table 1); CD 10551, right proximal humerus (Fig. 2a,b).

Description

CD 15667 is a complete isolated P⁴. It is a very robust tooth with a large protocone and parastyle and a very

Table 1. Dental specimens from Cooper's D and comparative modern and fossil measurements. L = mesio-distal tooth length, B = bucco-lingual tooth breadth. *Propoecilogale bolti* and *Poecilogale albinucha* data from Petter (1987, p. 230), *V. leakeyi* data from Hendeby (1973), *P. howelli* data from Morales *et al.* (2005). Site prefixes are as follows: Cooper's D – CD; Laetoli – LAET; Langebaanweg – L; Tugen Hills – BAR.

Species	Specimen	M ₁		P ⁴	
		L	B	L	B
<i>Propoecilogale bolti</i>	CD 3896	6.1	2.5		
	LAET 1358	5.6	2.5		
<i>Poecilogale albinucha</i> (modern, <i>n</i> = 5)		Mean 6.6 (range 5.8–7.2)	Mean 2.7 (range 2.2–3.0)		
<i>Civettictis cf. civetta</i>	CD 15667			14.1	11.2
<i>Viverra leakeyi</i>	L12863			17.4	11.1
	L20253			16.5	10.2
	L16224			17.3	10.5
<i>Pseudocivettictis howelli</i>	BAR 1812'01			12.8	9.5

pronounced lingual cingulum along the blade, with two small cusplets on it. It is similar in size to modern *Mellivora*, but the Cooper's D specimen has a much larger parastyle, a clearer protocone and a very prominent cingulum on the lingual surface. It is a very good match for modern *Civettictis civetta*, but there are some small morphological differences in the fossil specimen. The protocone is more robust and is markedly curved inwards towards the centre of the tooth, the parastyle is larger than most modern civets examined (*n* = 9) and the cingulum is larger and clearly delineated from the rest of the tooth by a deep channel. The two cusplets on the cingulum were also absent from all modern specimens examined.

CD 10551 is a complete proximal humerus with approximately one third of the shaft remaining. It is heavily encrusted with manganese dioxide, making measurements approximate, but the morphology is clearly visible. The trochanter has a sinuous or S-shaped curve when viewed superiorly, and there is a small ridge beneath the articulation on the dorsal surface which is only found in civets. It is an excellent match for a female *C. civetta* in the Ditsong Museum collections.

cf. *Civettictis* sp.

Material

CD 3263, a right distal radius (Fig. 2f,g); CD 1519, a left proximal 4th metacarpal (Fig. 2h,i).

Description

These specimens are more difficult to identify but are still most likely to represent cf. *Civettictis* sp. CD 3263 is a distal radius fragment that is heavily encrusted with manganese dioxide. In terms of size and general characters it is closest to civet and serval (*Leptailurus serval*); however, in the serval the articulation is broader medio-laterally, the styloid process is more defined and the shaft is more slender. In all of these features CD 3263 is closer to *C. civetta*. CD 1519 is a small proximal 4th metacarpal, which is also heavily encrusted with manganese dioxide, making the morphology difficult to determine. However, the position of facets for the 3rd metacarpal indicate that it is not

caracal (*Caracal caracal*), and it is too narrow dorso-ventrally to be serval. A small depression on the proximal ventral surface of the shaft is also present in *Civettictis*, and it has therefore been referred to that genus.

Discussion

Of the material that has been confidently assigned to *Civettictis*, the P⁴ indicates an animal that is more robust than the modern civet, while the humerus is almost identical to a modern specimen. The P⁴ differs from *Pseudocivetta howelli* from Tugen Hills, Kenya (Morales *et al.* 2005; Morales & Pickford 2011), as the Cooper's D fossil is larger (Table 1) and has a markedly greater distance between the protocone and the paracone, and the cingulum is smooth and much less defined in the Kenyan specimen. In addition, the buccal border of the P⁴ (as illustrated in Morales & Pickford (2011)) in both *Pseudocivetta howelli* and *Pseudocivetta ingens* is almost straight, while in *C. civetta* and CD 15667 there is a clear dip inwards at the carnassial notch. In comparison with the only other large viverrid craniodental remains known from South Africa, *Viverra leakeyi* from Langebaanweg (Hendeby 1974b, pp. 75–83), the Cooper's P⁴ is substantially smaller in length, but is its equivalent in breadth (see Table 1), and the cingulum is even less developed in *V. leakeyi* than it is in modern *C. civetta*. Prior to the Cooper's D excavation, the only viverrid material identified from the Witwatersrand sites was a humerus from Kromdraai B (Hendeby 1973). While Hendeby (1973) did not identify it to genus or species, he noted that it was morphologically indistinguishable from both *C. civetta* and *V. leakeyi*. Brain (1981) referred the same specimen (KB 3258) to *Viverra* sp., but it has recently been reassigned to *Mellivora* sp. (Gommery *et al.* 2008). The reassignment of this single specimen means that currently Cooper's D is the only Witwatersrand site to have a record of a civet. As there is a paucity of fossil *Civettictis* material in Africa, we have assigned both the cranial and postcranial specimens to *Civettictis cf. civetta* as they are clearly very closely related to the modern species.

Discussion of Cooper's D Mustelids and Viverrids

A minimum number of one individual of each of the genera *Civettictis*, *Propoecilogale* and *Mellivora* are present

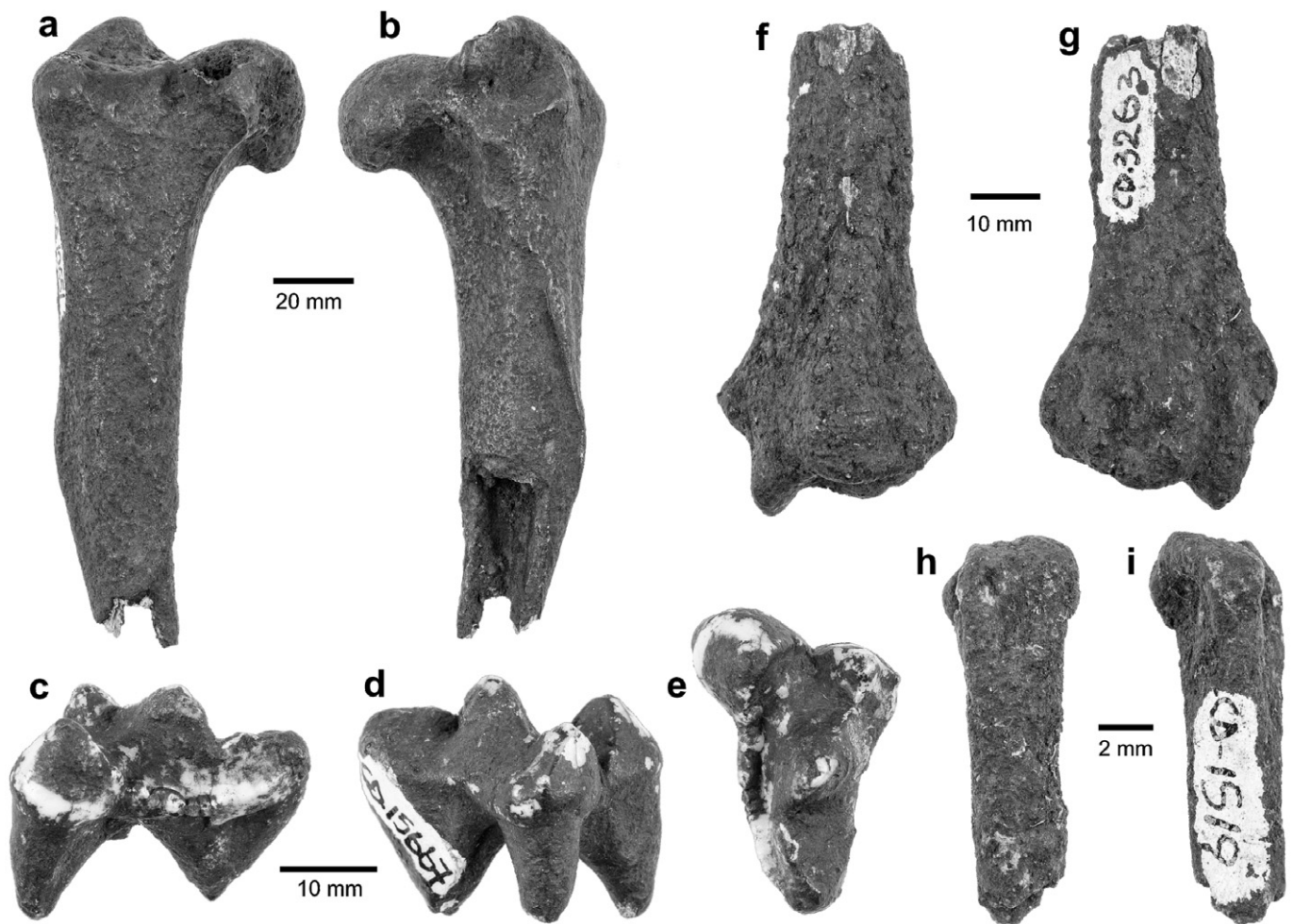


Figure 2. Viverrid material from Cooper's D. Specimens attributed to *Civettictis* cf. *civetta* are: CD 10551, a proximal right humerus in medial (a) and lateral (b) views, and CD 15667, a left P⁴, shown in lingual (c), bucco-mesial (d) and occlusal (e) views. Specimens referred to cf. *Civettictis* sp. are CD 3263, a right distal radius in dorsal (f) and ventral (g) views, and CD 1519, a left proximal 4th metacarpal showing the articulation for the 5th metacarpal (h) and a dorsal view (i). Both of these specimens are heavily encrusted with manganese dioxide.

at Cooper's D (Table 2). They are rare both within the deposit and in the wider African fossil record. Of the three genera described here, the remains of *Mellivora* spp. are most commonly found as fossils in Africa, with specimens reported from 20 localities (Werdelin & Peigné 2010). These include five localities with material referred to *Mellivora benfieldi*, first described from Langebaanweg by Hendeby (1978), and discussed by Petter (1987) as a possible ancestor to the modern *M. capensis*. To Werdelin & Peigné's (2010) list can be added: the specimen reassigned by Gommery *et al.* (2008) from Kromdraai B, the cranio-dental fragments recorded from Swartkrans Member 2 by Brain (1981), and our new identification of *M. capensis* from Cooper's D. This substantially increases our knowledge of the genus at the Witwatersrand sites during the

early Pleistocene. Honey badgers are widely distributed across Africa, in habitats from dense forests to deserts (Larivière & Jennings 2009).

The second mustelid species, *Propoecilogale bolti*, is an extremely rare taxon. In addition to our new identification at Cooper's D, this species has been identified at Ahl al Oughlam (as *Prepoecilogale* sp. cf. *P. bolti*), in Morocco (Geraads 1997), at Bolt's Farm in South Africa (Cooke 1985), and in the Upper Unit of the Laetoli Beds, Laetoli, Tanzania (Werdelin & Peigné 2010). This very wide but sparse geographic range may be more indicative of sites that have been sieved (Geraads 2008) or that have good preservation of smaller bones, rather than relating to the scarcity of the animal. The modern species *Poecilogale albinucha* is associated with moist to dry savanna (Skinner & Chimimba 2005), but too little is known of the extinct *P. bolti* to ascertain its environmental preferences.

With the possible exception of genets, viverrid remains occur infrequently in the African fossil record, and when found they are often referred to Viverridae indet. (Werdelin & Peigné 2010). Members of the genus *Civettictis* have been reported from five sites across East and South Africa, but only one has been confidently assigned to the modern species *C. civetta* (Werdelin & Peigné 2010). As discussed

Table 2. Number of specimens identified for each taxon (NISP), and minimum number of individuals represented by the material (MNI).

Taxon	NISP	MNI
<i>Propoecilogale bolti</i>	1	1
<i>Mellivora capensis</i>	1	1
<i>Civettictis</i> cf. <i>civetta</i>	2	1
cf. <i>Civettictis</i> sp.	2	–

above, the proximal humerus matches the modern material very well, but there are features of the P⁴ that have led us to describe it as *Civettictis* cf. *civetta*. Following the reassignment of the Kromdraai B humerus, the specimens from Cooper's D are the only civets to have been identified from the Witwatersrand sites. Gauteng lies on the southernmost edge of the modern civet's range (Skinner & Chimimba 2005). The extant African civet lives in 'forest and open habitats (particularly with dense ground cover)' and is also 'associated with riverine habitat in drier regions' (Jennings & Veron 2009, p. 210), and Ray (1995) reports that it has been found between sea level and up to 5000m. However, in southern Africa it is found largely in 'forest and well-watered savannah' (Skinner & Chimimba 2005). It is omnivorous with dietary habitats differing by region and by season (Jennings & Veron 2009). Thus the presence of a civet at Cooper's D may indicate some dense vegetation and/or water in the vicinity of the site.

The three taxa reported here do not help to refine our understanding of the palaeoenvironment at Cooper's D, as the two extant species have wide ecological tolerances, and the third (*Propoecilogale bolti*) is very poorly known.

CONCLUSION

The viverrid and mustelid material described here expand the known fossil distribution of these relatively rare taxa at a well-dated (1.5–1.4 Ma) locality in southern Africa. The African civet *Civettictis* cf. *civetta* is the first to be reported from any of the Gauteng sites, and the Cooper's D assemblage also provides further evidence for the presence of the honey badger and *Propoecilogale* in the Witwatersrand region. This work emphasises the importance of examining all material, including postcrania, from a site and equally the importance of sieving the deposits to retrieve rarely-found and smaller taxa such as *Propoecilogale*.

The authors would like to express their appreciation to the Ditsong National Museum of Natural History and the Evolutionary Studies Institute at the University of the Witwatersrand for access to their comparative collections. In particular, we thank Teresa Kearney, Curator of the Modern Small Mammal collection, Shaw Badenhorst, Curator of the Archaeozoology and Large Mammal Section, and Stephany Potze, Collections Manager of the Palaeontological collections at the Ditsong National Museum of Natural History, and Bernard Zipfel, Senior Collections Curator at the Evolutionary Studies Institute, for their assistance. This study was financially supported by awards to B.F.C. from the Palaeontological Scientific Trust (PAST), the South African National Research Foundation and the University of the Witwatersrand Postgraduate Merit Award. C.M.S. thanks PAST for funding the initial excavation during which most of the specimens were found. HO'R's research on the Cooper's D Carnivora was supported by a Liverpool John Moores University Early Career Researcher Award in 2010, and PAST in 2008.

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